A REVIEW OF THE SPECIES OF *SCARITES* (*ANTILLISCARIS*), (COLEOPTERA: CARABIDAE) WITH NOTES ON THEIR MORPHOLOGY AND EVOLUTION

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Recently, through the courtesy of Prof. R. A. Howard, Director of the Arnold Arboretum at Harvard University, the Museum of Comparative Zoology received a shipment of Coleoptera from the Luquillo Mountains of Puerto Rico, collected on "W. Peak" by R. A. McClain. Included in this material was a single specimen of the largest carabid in the Greater Antilles, representing a new species of *Scarites (Antilliscaris)*, 35 mm in length. This behemoth is superficially different from but shares a unique set of characters with two known species of the subgenus from the mountains of Puerto Rico. The presence in the depauperate Puerto Rican montane carabid fauna of three species of *Scarites* raises questions about the ecology and evolution of these beetles. These questions have been approached through study of the comparative functional morphology of *S. (Antilliscaris)* and other *Scarites* subgenera and through preliminary observations and experiments on one adult collected during a recent trip to Puerto Rico.

Banninger (1949, p. 146) proposed the subgenus *Antilliscaris* for *Scarites darlingtoni* Banninger, *S. mutchleri* Banninger (both orig-

inally considered to be of uncertain systematic position, 1939, p. 148) and for *S. danforthi* Darlington. Banninger incorporated the new subgenus into his earlier key to the subgenera of *Scarites* (1937, pp. 123-128) and provided a key to separate the species.
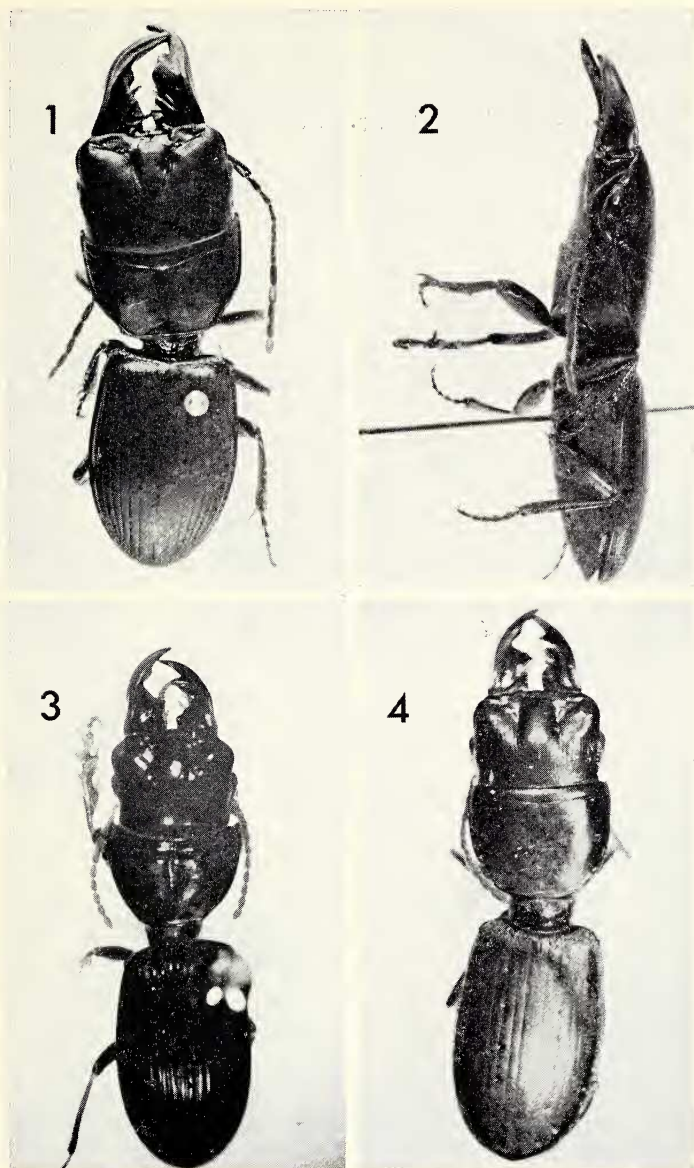
Scarites subgenus *Antilliscaris* Banninger 1949, p. 136

Diagnosis: head: large, 37-59% of length of elytra. *Mandibles:* median carnassal regions large, basal molar area small with complex of interdigitating cusps, dorsal surface smooth. *Eyes:* small, height 30-50% of height of mandible. *Antennae:* long to very long for a *Scarites*, segment 4 similar to apical segments, dorsal and ventral setose areas with rough microsculpture and pair of narrow lateral glabrous regions without setae, sides flattened but not as distinctly as in segments 5-11. Segment 3 circular in cross section with apical ring of setae as well as a number on the apical 2/3 of the dorsal surface and a few setae, including some very large ones on the ventral surface (Fig. 13). Frontal plate grooved. *Pterothorax:* metasternum and metepisternum short, L/W of episternum 0.87-1.3, elytra fused together and to mesanotum, wings reduced, shorter than metanotum in *mutchleri*. Lateral edge of mesotibia with one large spine. *Metepimeron:* slender, pleural suture very faint externally; epimeron-elytra interlocking mechanism absent.

Distribution: montane rain forests of Puerto Rico.

Key to the species of *S. (Antilliscaris)* and to *S.* (?) *darlingtoni* Banninger

1. Mandibles with series of striations on dorsal surface (Fig. 7) .... *darlingtoni*
1′ Mandibles: dorsal surface smooth (Figs. 6, 10, 11) 2
2. Elytral intervals 1, 3, 5 and 7 with setiferous punctures. Dorsal surface of head with 15 setiferous punctures. Antennae short, extending about to posterior border of prothorax, L/W of segments 6-10 less than 1.1 (Fig. 8) .... *danforthi*
2′ Only elytral interval 3 with setiferous punctures. Dorsal surface of head with 6 or fewer setiferous punctures 3
3. Antennae extending to mesocoxae, L/W of segments 6-10 between 1.3 and 1.6 (Fig. 9). Slight impression at posterior end of scrobe. Lateral margin of pronotum with 5-6 pairs of setiferous punctures, L/W 0.80. Total length 12-18 mm .... *mutchleri*
3′ Antennae extending to first abdominal sternite, L/W of segments 6-10 between 1.8 and 2.3 (Figs. 11, 12). Deep pit at posterior end of scrobe. Lateral margin of pronotum with 3 pairs of seti-

Figs. 1, 2 — *S. (Antilliscaris) megacephalus* n. sp. Fig. 3 — *S. (A.)* *danforthi*. Fig. 4 — *S. (A.) mutchleri*.

ferous punctures, L/W 0.54. Total length 30-35 mm. ....

.... *megacephalus* n. sp.

Scarites (*Antilliscaris*) *mutchleri* Banninger

Scarites mutchleri Banninger 1939, p. 149, replacement name for *montanus*
  Mutchler 1934, not *montanus* Banninger, 1932.
Scarites montanus Mutchler 1934, p. 1.
Type: American Museum of Natural History, seen; type locality: Puerto
Rico, Luquillo Mtns., El Yunque, 1800 ft.

Description (diagnostic characters only). With the characteristics
of the subgenus *Antilliscaris*. Forms as in Fig. 4. *Head:* antennae
long, extending to about middle of peduncle, apical segments inter-
mediate between *danforthi* and *megacephalus*, L/W of segments 4-10
between 1.3 and 1.9 (Fig. 9). *Vertex:* 3 pair of setae, clypeal, supra-
orbital and a pair halfway between the two and closer together than
either. Lateroclypeus and antero-lateral halves of vertex with a
series of irregular striations. Without a large depression behind the
eye and a deep pit at the posterior end of scrobe. *Prothorax:* lateral
grooves narrow but distinct with 5 or 7 pairs of setiferous punctures,
posterior angles small. *Sternum:* 6-8 setiferous punctures clustered
in front of the intercoxal spine, the latter with 6-8 setae. *Elytra:*
surface dull, anterior margin with dense band of coarse tubercles in
addition to the tubercles associated with setiferous punctures. *Lateral
groove:* dense concentration of tubercles, 7-8 setiferous punctures on
third interval. Striae lightly impressed. *Pterothorax:* mesasternum,
2 setiferous punctures; metasternum 6-7 setiferous punctures. *Ab-
domen:* 1st and 2nd intersegmental sutures normal.

Measurements. *Head:* length 2.7-3.1 mm, width 3.6-4.0, length/
width 0.75-0.77. *Mandible:* length 2.3-3.0. *Prothorax:* length 3.1-
3.5, width 4.0-4.6, length/width 0.77-0.76. *Elytra:* length 6.9-7.9,
width 4.2-4.8, length/width 1.64-1.64. Total length (including
peduncle) 15.4-18.0 mm. *Measurements reported:* extremes in total
length of the four specimens measured. *Specimens examined:* holo-
type and three others (M.C.Z.). A specimen, currently alive, about
12 mm in total length, has not been examined critically.

Distribution: El Yunque, 1800 ft. to summit (3493 ft.).

Larva: Three presumably second instar *Scarites* were collected
on El Yunque, one in a decayed log in cloud forest c. 2200 ft., and
two others under rocks along a forest trail c. 3200 ft. Based on
size (head capsule of preserved larve 1.9 mm wide) these larvae are
probably *mutchleri*.

Scarites (Antilliscaris) megacephalus n. sp.

Holotype: a male M.C.Z. No. 31710. *Type locality:* Puerto
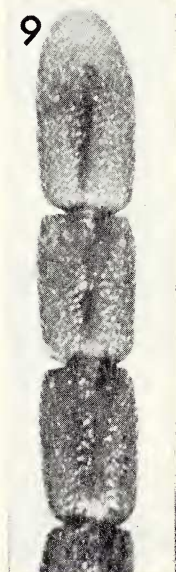
Fig. 5 — Mandibles, *S. (s. s.) substriatus*. Fig. 6 — Mandibles, *S. (A.) mutchleri*. Fig. 7 — Mandibles, *S. (?) darlingtoni*. Fig. 8 — Antennal apex, *S. (A.) danforthi*. Fig. 9 — Antennal apex, *S. (A.) mutchleri*.

Rico, Luquillo Mountains, top of West Peak, 3447 ft., May or June 1968, W. C. McClain Coll. *Paratype:* M.C.Z.; Sex ?, El Yunque *c.* 3200 ft., Feb. 1969, L. H. Herman Jr., B. C. and T. F. Hlavac collectors. This fragmented specimen, missing the antennal flagella, maxillae, several legs and the apical abdominal segments, was collected dead under a stone along a forest trail.

Description (diagnostic characters only). With the characteristics of the subgenus *Antilliscaris* (form as in Figs. 1, 2). *Head:* very large as compared to the relatively squat pronotum and elytra. Antennae very long, extend to first abdominal sternite, length/width of segments 4-10 between 1.8-2.3 (Fig. 12). *Vertex:* pair of clypeal and supraorbital setiferous punctures. With a deep, broad depression behind the eye and a deep puncture at the posterior end of the scrobe. Lateroclypeus and antero-lateral halves of vertex with series of irregular situations. *Prothorax:* lateral grooves narrow but distinct with 3 pairs of setiferous punctures (4 on left side of paratype). Sternum without setiferous punctures, intercoxal spine with 12. *Elytra:* surface dull. *Anterior:* margin with small number of minute tubercles about 1/3 the width of those associated with punctures; 1 pair of setiferous punctures in third interval, striae strongly impressed. Mesasternum with 2 setiferous punctures, metasternum with 4. *Abdomen:* lateral portions of 1st and 2nd intersegmental sutures broadened and deepened to form a large fossa, sutures separating other segments slightly enlarged laterally.

Measurments of holotype and paratype: Head: length 7.5-7.1 mm, width 9.5-7.2 length/width 0.79-0.98; *Mandible:* length 7.0-5.7; *Prothorax:* length 5.5-5.0, width 10.1-8.1, length/width 0.54-0.62; *Elytra:* length 13.0-12.5, width 9.3-7.9, length/width 1.4-1.58; *Total length (including peduncle):* 35-30 mm.

Distribution: known only from the type series.

Scarites (Antilliscaris) danforthi Darlington

Scarites danforthi Darlington 1939, p. 80.
Type: M.C.Z. No. 23,501 seen; type locality: Puerto Rico, Maricao forest, *c.* 3000 ft.

Description (diagnostic characters only). With the characteristics of the subgenus *Antilliscaris*, form as in Fig. 3. *Head:* antennae, relatively short, extend to posterior margin of prothorax, apical segments squat, L/W of segments 4-10 less than 1.1 (Fig. 8). Vertex with 15 setiferous punctures including 2 pair of supraorbitals. Lateroclypeus and anterolateral halves of vertex without series of irregular situations. Without a large depression behind eye and deep pit at posterior end of scrobe. *Prothorax:* lateral groove indistinct near

Fig. 10 — Mandibles, *S. (A.) danforthi*
Fig. 11 — Mandibles, *S. (A.) megacephalus* n. sp.
Fig. 12 — Antennal apex, *S. (A.) megacephalus* n. sp.
Fig. 13 — Antennal segments 3, 4, 5, *S. (A.) megacephalus* n. sp.

middle, with 5 pairs of setiferous punctures, posterior angles very small. *Sternum:* about 20 setiferous punctures clustered about the midline, intercoxal spine with 10-12 setiferous punctures. *Elytra:* surface shiny. *Anterior margin:* small number of minute tubercles 1/3 the width of the tubercles associated with setiferous punctures, 4 or 5 setiferous punctures in first interval, 7 or 8 in third, 6, 7, or 8 in fifth, and 5, 6, or 7 in seventh, striae lightly impressed. *Pterothorax:* mesasternum 8 setiferous punctures, metasternum 6 setiferous punctures. *Abdomen:* lateral parts of 1st and 2nd intersegmental sutures broadened and deepened to form a large fossa, other sutures enlarged laterally.

Measurements of holotype and paratype. Head: length 2.5-3.0 mm, width 3.1-3.5, length/width 0.81-0.86. *Mandibles:* 2.2-2.6. *Prothorax:* length 2.7-3.0, width 3.9-4.0, length/width 0.69-0.67. *Elytra:* length 6.7-6.7, width 4.0-4.0, length/width 1.68-1.68. Total length (including peduncle) 14.6-16.0.

Distribution: known only from the type series.

Scarites (subgenus?) *darlingtoni* Banninger

Scarites darlingtoni Bann. 1935, p. 159.
Scarites (Antilliscaris) darlingtoni Bann. 1949, p. 137.
Type: M.C.Z. No. 21,797, seen. Type locality: N. Haiti, Mt. Basil, *c.* 4700 ft.

Description (diagnostic characters only). *Head:* large, 43% of the length of the elytra. Mandibles (Fig. 7) heavily worn in type, with striate dorsal surface and relatively small molar area. *Eyes:* 50% of the height of the mandible. *Antennae:* absent in type. Lateroclypeus and antero-lateral halves of vertex with series of irregular striations. *Vertex:* pair of clypeal and supraorbital setiferous punctures. Without depression behind eye and large puncture at posterior end of scrobe. *Prothorax:* lateral grooves distinct with 7 or 8 setiferous punctures. *Sternum:* without setiferous punctures but with 17 on intercoxal spine. *Elytra:* surface polished. Anterior margin with small number of tubercles about 1/3 the width of those associated with punctures. Lateral groove rugose. 8 setiferous punctures in third interval, striae impressed. *Pterothorax:* reduced, elytra fused together and to mesanotum, wings shorter than the metanotum. Metepisternum and metepimeron absent in type, L/W about 1. Mesasternum without setae and metasternum with 6. *Abdomen:* intersegmental sutures normal.

Measurements of holotype: Head: length 4.0 mm, width 5.1, length/width 0.78. *Mandible:* length 3.0. *Prothorax:* length 4.0, width 5.6, length/width 0.72. *Elytra:* length 9.5, width 6.3, length/

width 1.50. Total length (including peduncle) 21.8. *Specimen examined:* holotype.

Comments: known from the appendageless fragments of two specimens. I regard it as of uncertain subgeneric position for three reasons. The structures containing the major diagnostic characters of *Antilliscaris,* antennae and metepimeron, are absent in the available material. A major similarity between *Antilliscaris* and *darlingtoni* is the reduction of the flight mechanism. Flightlessness and, *in extenso,* large-scale reorganization of the flight mechanism occur with high frequency among montane carabids (Darlington 1943), which argues against uniting *darlingtoni* with *Antilliscaris* in the absence of other evidence. Furthermore, there is a gap between *Antilliscaris* and *darlingtoni* in the dorsal surface of the mandibles (Figs. 5, 6, 7, 10, 11).

DISCUSSION

Several character states in *Antilliscaris* range from atypical to unique for a *Scarites s. l.* Many of these differences are found in the locomotory system or are peripheral to it. This raises questions about associated behavioral and ecological differences. In an attempt to list some of the possible answers to these questions, particular configurations of *Antilliscaris* are contrasted with *S. (s. s.) substriatus* Haldemann and *subterraneus* Fabricius. This is not done because I feel that these 2 species are closely related to *Antilliscaris,* but because both fly and burrow (Hlavac, 1967) and can be used as a base line in interpreting the morphology of *Antilliscaris.*

ANTENNAE: The antennae of *Antilliscaris* are unusual in three respects: in length, in the setation of the 4th segment and in the relative narrowness of the lateral glabrous areas. An increase in the size of the antennae can be documented in terms of elongation of individual segments, as expressed by length/width, and in terms of increase relative to body size. The ranges of length/width of segments 6-10 is 0.9-1.1 in *danforthi,* 1.35-1.55 in *substriatus,* 1.3-1.6 in *mutchleri,* and 1.8-2.3 in *megacephalus.* The antennae reach the procoxae in *substriatus,* the posterior margin of the prothorax in *danforthi,* and middle of the peduncle in *mutchleri* and the first abdominal sternite in *megacephalus.* As compared to *substriatus,* the antennae of *danforthi* are longer and the individual apical segments are much wider. Assuming that there are no major differences between the relative widths of the first segment in the above species, then a measure of width of the antennal apex can be expressed as width of an apical segment/width of segment 1. Using width of the 8th segment in this ratio, the figures are 0.72 for *substriatus* and *megacephalus,* 0.93 for *mutchleri* and 1.1 for *danforthi.*

To summarize, the antennae of all *Antilliscaris* are longer than *substriatus*. The apical segments are broad in *danforthi*, elongate in *megacephalus*, with *mutchleri* and *substriatus* intermediate.

In *substriatus*, 28% of the antennae extends beyond the mandible. When burrowing the antennae are held agaist the head wall causing the apical segments to curve in a broad U. In *megacephalus* 50% of the antennae extends beyond the mandible. If this species burrows the antennae would be doubled over while the animal is working. Short antennae are characteristic of the many diverse taxa of burrowing Coleoptera which have independently evolved a pedunculate body form. The long antennae of *Antilliscaris* and particularly *megacephalus* strongly suggests that these beetles do not burrow.

Captive *substriatus* and *subterraneus* and many geophilious carabids apparently do not react visually to prey; olfactory and/or tactile reactions have been observed upon physical contact. While patrolling a burrow system, the antennae of *subterraneus* are held parallel to the long axis; the maximum sweep width is limited by the diameter of the burrow. On the surface, they are held approximately 45° from the long axis. If only short range olfactory and tactile stimuli are used to recognize prey, then finding it will be a function of the distance travelled and the width of the band through which the sensory equipment move. On the surface, long antennae are clearly adaptive in increasing the width of the search band, and may partially explain the condition in *Antilliscaris*.

There is a gap in the setation and microsculpture of the first 4 segments as contrasted to segments 5-11 in all subgenera except *Antilliscaris* and *Typhloscaris* from the mountains of E. Africa. In most subgenera, segments 1-4 have few or no setae and are circular in cross section, while segments 5-11 are flattened laterally and have a dense covering of setae and rough microsculpture except for a glabrous, asetose median stripe. Segment 4 of *Antilliscaris* is intermediate in shape between segments 3 and 5 and has the surface organization of the apical segments.

The surface of the apical segments is divided into two distinct structural and, probably, functional areas. As seen in lateral view, a pair of setose bands with rough microsculpture extend along the dorsum and venter of the apical segments; they are united near the distal end of the 11th segment (Figs. 8, 9, 12). Between the setose bands is an asetose median band with smooth microsculpture. Members of the genus *Scarites* differ widely in the distribution of these two surface types; in *S. (Antilliscaris)* the median band is 25-30% of the width, but 55% in *substriatus*.

The elongate and/or broad apical segments and the state of the 4th segment in *Antilliscaris* represent an increase in surface area of antennal apex over *substriatus*. Due to differences in distribution of surface types, there is a large increase in setose areas, which can be interpreted as an intensification of the functions served by this region.

EYES: The eyes of *Antilliscaris* are small, 30-50% the height of the mandible, vs. 100% in *substriatus*, and are nearly circular except in *danforthi* where the posterior border is nearly straight. Smith (1964, p. 116) stated that the eyes of flightless carabids are not reduced, except for cave inhabiting species; this is clearly not the case for montane *Scarites* or for the montane carabid fauna of New Guinea (P. J. Darlington Jr., personal communication). Eye reduction in *Scarites* seems to have come about either from a reduction in diameter *(Antilliscaris)* or from diameter reduction and shortening the anterior posterior axis, giving the eyes of *S. (Typhloscaris)* and *S. (Taeniolobus) cubanae* Banninger a peculiar slit-like appearance.

MANDIBLES: The mandibles of scaritine carabids are structurally complex and can be divided into three functional regions, an apical and 2 medial carnassal areas and a basal molar part. *Antilliscaris* and *Scarites s. s.* represent extremes in the relative sizes of the latter 2 of these areas (Figs. 14, 15). In an unworn specimen of *substriatus* (Fig. 5) the apical carnassal is 34%, the median carnassals 26% and the molar 40% of the total length (perpendicular distance between apex and base); while in *Antilliscaris* (Figs. 6, 10, 11) the apical carnassal ranges from 24-34% the median carnassals from

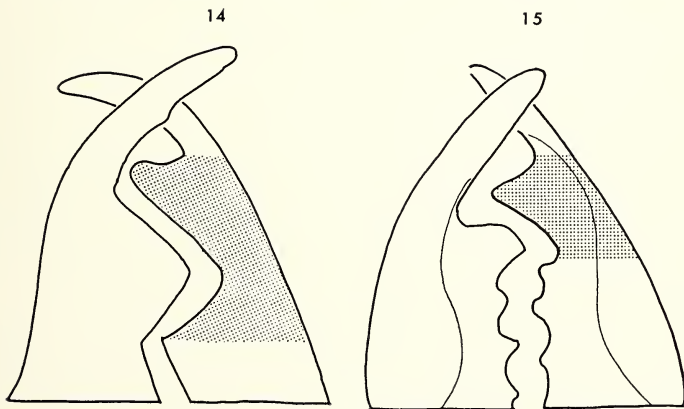14   15

Fig. 14. — Mandibles, *S. (Antilliscaris)*. Fig. 15 — Mandibles, *S. (s. s.)*. Medial carnassal areas shaded.

45-59% and the basal molar part ranges from 17-21% of the total
length. In *Antilliscaris* then, the median caranassals are twice as
large and the molar area half the relative size of the corresponding
areas of *substriatus*.

If it can be assumed that these structural differences correlate with
behavioral differences, then the condition in *Antilliscaris* may reflect
3 types of such differences. The mandibles of *substriatus* and *sub-
terraneus* are used to loosen material from the head wall of the bur-
row, in mating and, of course, in feeding. Some substrate loosened
by the protibia is compressed further and compacted into a part
of the stable burrow system by the vertex of the head and pronotum
(Hlavac, 1967, and unpublished observations). The smaller molar
area in *Antilliscaris* could indicate either that these animals burrow
through a less dense, more easily compacted, substrate than *Scarites
s. s.* or that they do not burrow at all. Secondly, the differences in
mandible morphology may reflect differences in feeding behavior (see
comments on body form, below) or mating.

FLIGHT MECHANISM: *Antilliscaris* represents an extreme point in
the atrophy of the flight mechanism. The fused elytra are immovably
joined to the mesathorax at two points, the posterior part of the
mesatergum is tucked around and closely pressed against the anterior
contours of the elytral cavity and secondly, the elytral hinge mech-
anism is solidly fused to the anterior part of the mesatergum.

The volume enclosed by the metathorax is reduced; externally,
this is seen most clearly by comparing the relative size of the lateral
portion of the sternum and the L/W ratio of the episternum in
flying and wingless species. In *substriatus* the narrowest lateral part
of the sternum is about half the mid-line length and the L/W of
the episternum is about 4, whereas in *mutchleri* the lateral portion
is 20% of the mid-line length and the L/W of the episternum is
about 1. The central part of the sternum is also shortened in *Antil-
liscaris* but less dramatically; the mid-line in *substriatus* is equal to
the length of tthe first 3 1/2 abdominal sternites while in *mutchleri*
it is equal to the length of the first 2 2/3 abdominal segments. The
vestigial wings of *mutchleri* are very small (.375 × .100 mm) and
circular in cross section in a specimen examined in fluid.

In the Scaritini there are usually 3 lateral elytra-thorax and abdo-
men interlocking mechanisms. (Hlavac, unpublished observations.)
The anterior lateral edges of the elytra fit into grooves on the dorsal
rim of the mesepisternum, mesepimeron and metepisternum (Fig. 17).
The dorsal part of the metepimeron slopes inwards; the elytra curve
slightly outwards at this point and rest on top of the flat surface of

the epimeron. An internal elytral carina extends from just behind the level of the epimeron to the elytral apex and is enlarged posteriorly forming the internal plica. The carina rests against the edge of the infolded abdominal sternites.

Antilliscaris differs from all other subgenera of *Scarites* examined, including many flightless species, in that the dorsal part of the metepimeron is in the same plane as the episternum and the dorsal groove extends along the epimeron, i. e. the elytra-epimeron interlocking mechanism is absent, becoming part of the elytra-episternum device (Fig. 18).
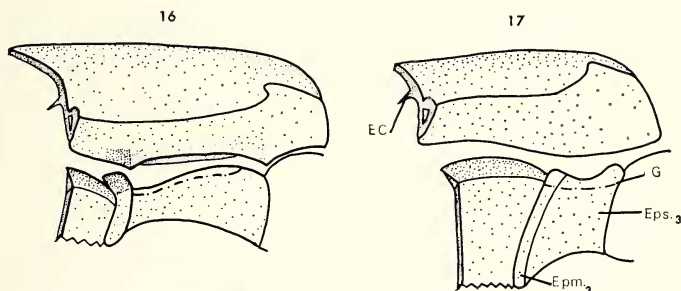

Fig. 16 — Elytra-metathorax interlocking mechanism S. (s. s.) substriatus
Fig. 17 — Elytra-metathorax interlocking mechanism, S. (Antilliscaris) (EC, internal carina of elytra; Epm$_3$, metepimeron; Eps$_3$, metepisternum; G, metapleural groove)

In burrowing and substrate dwelling Coleoptera, the elytral interlocking mechanisms maintain the structural integrity of the elytrabody joint against the forces generated in moving through a dense material. Lack of an integral portion of this mechanism in *Antilliscaris* can be explained in two, non-mutually exclusive manners. If the ancestral stock were not a highly adapted burrower (see below), then loss of epimeron-elytra joint could be due to neutral selection pressure for structural integrity. Or, secondly, after becoming flightless, the primary interlocking mechanism becomes the fusion of the elytra to each other and to the mesothorax; loss of epimeron-elytra joint represents post-adaptational adjustment; there is no need to assume a change in selection pressure for structural integrity.

BODY FORM: *S. (A.) megacephalus* and *S. (s. s.) substriatus* represent extremes in body proportions with *mutchleri* and *danforthi* intermediate. The outline of *megacephalus* can be derived from that of *substriatus* by shortening the pterothorax and abdomen (Elytra L/W from 1.8 to 1.4 in *S.* and *A.* respectively) and the prothorax

(L/W from 0.7 to 0.5) and by increasing the size of the head until it is 1.36 the length of the prothorax (0.82 in *substriatus*) and until the length of head and mandibles is 1.1 the length of the elytra (0.6 in *substriatus*).

A partial explanation of the shortening of the elytra is the atrophy of the flight mechanism. Differences in size between the head and prothorax can be looked at in terms of differences in muscle volume, i. e., a relative decrease in volume in the prothorax and a relative increase in the head. The prothorax houses most of the muscle volume responsible for its movement as well as that which moves the head and proleg (Larsen, 1966, p. 140), while the head encloses muscles responsible for the movement of its appendages. Ventrodorsal rotation of the head and prothorax are principal actions in burrowing, decrease in muscle volume for performing these actions indicates a shift in or absence of burrowing behavior. The large head implies a large mandibular adductor muscle and this along with the large carnassal areas of the mandibles could be an adaptation for seizing and breaking open large prey objects.

ECOLOGICAL SHIFT: Of the eight known montane species of carabids on Puerto Rico listed below, three are *Scarites*, and, with *Oxydrepanus coamensis* Mutchler, scaritines make up 50% of the known carabid fauna. On Jamaica, an island of similar size (4500 sq. mi. vs. 3400 for P. R.) 17 montane restricted species are known, nine of which are *Colpodes*; there are no *Scarites* (Darlington, 1941). As currently known, the montane biota of Puerto Rico is unique in the Greater Antilles in not having a large number of ecologically variable *Colpodes*. The size range of Puerto Rican species is 2.0 to 35 mm with the following distribution:

1-5 mm, 4 spp.,	*Oxydrepanus coamensis* Mutchler, 2 mm;
	Bembidion portoricense Darlington, 3.5 mm;
	Perigona microps Darlington, 2.9 mm;
	Phloeoxena portoricensis Darlington, 4.5 mm.
5-10 mm, 1 sp.,	*Colpodes estriatus* Darlington, 4.0-6.7 mm.
10-20 mm, 2 spp.,	*Antilliscaris danforthi*, 14.6-16.0 mm;
	Antilliscaris mutchleri, 12.0-18.0.
30+ mm,	*S. (A.) megacephalus*, 30-35 mm.

Antilliscaris is thus the largest carabid taxon, is at the apex of the size pyramid and is doubtless one of the top predators among ground invertebrates in this habitat.

It is useful to look at the mountains of Puerto Rico as habitat islands and to analyze the large *Scarites* fauna in the manner of MacArthur and Wilson (1967). In harmonic continental biotas,

the large number of carabid species occupy three locomotory adaptive zones: arboreal (several tribes), ground in the broadest sense including soil surface and leaf litter (most tribes and species) and burrowing (primarily the Scaritini). All terrestrial zones available to a beetle are exploited by the Carabidae. Breadth of adaptation for the family and high local diversity (see Darlington 1943 for data) is the result of adaptive radiation and species packing via competition. The energetics of food searching differs between the zones. If the energy expended by a ground species in searching a unit area is taken a base point, then both arboreal forms, which fly and climb vertical surfaces, and burrowers producing a new section of burrow expend more. In the absence of competition from related taxa, as in the mountains of Puerto Rico for a large carabid, if ecological shift occurs in a new colonizer it should be in the direction of increased efficiency of search behavior.

The burrowing mechanism of Scaritine carabids consists of many interrelated morphological and behavioral adaptations. Evidence that several structures and proportions differ from a known burrow producer is presented above and can be interpreted as indicating a reorganization of the burrowing mechansm for a ground surface existence.

The steps taken by a species after colonizing a depauperate habitat island are: initial adaptation, ecological shift, loss of dispersal power, speciation, and adaptive radiation (MacArthur and Wilson 1967, Chap. 7). Speciation and loss of dispersal power have occurred in *Antilliscaris*; there is evidence for ecological shift. That an adaptive radiation has occurred in *Antilliscaris* is an exciting possibility and should stimulate further field work.

BEHAVIOR: A specimen of *S. (A.) mutchleri* is currently being observed. While a full report of its behavior is planned, the following observations are germane at this point. The beetle has not constructed an elaborate burrow system under conditions where *substriatus* and *subterraneus* would (Hlavac 1967). Daylight hours are spent under retreats or in concealment burrows, about 2 body lengths long, dug in areas where the soil has not been highly compressed. During the night, this animal has eaten food placed on the surface and fallen into a small pitfall trap in the center of the container 24 nights out of 37. These fragmentary data are consistant with the hypothesis of ecological shift.

BIOGEOGRAPHY: The factors responsible for the high frequency of wing atrophy in montane carabids have been analyzed by Darlington (1943). He pointed out (1939, pp. 79-80) that mountains over

5000 ft. high on Cuba, Jamaica, and Hispaniola have endemic montane species that had become -winged on the spot. Noting that three -winged stocks on the mountains of Puerto Rico (*Antilliscaris*, *Oxydrepanus* and *Colpodes estriatus* Darl.) were closely related to forms known only from the mountains of Haiti, he concluded that each had reached Puerto Rico from Haiti after becoming flightless, and that mountains lower than 4000 ft. in the Antilles "are too low to induce wing atrophy among Carabidae." *S. darlingtoni* was here held to be closely related to the known species now in *Antilliscaris*. While I consider this species to be *incertae sedis* at the subgeneric level, the evidence for so doing (see systematic treatment) is not overwhelming, and this decision mainly reflects caution. In any case, questions as to the point of origin and the site of wing atrophy remain.

Long distance dispersal of montane forest-floor-inhabiting, flightless carabids to another suitable montane environment must be a rare event. Such species have all "bad" attributes that preadapt a species to be "good" colonizers (MacArthur and Wilson 1967, p. 81). Flightless carabids are rare in the tropical lowlands (Darlington 1943, pp. 44, 49-50) and would be severely selected against in areas subject to flooding. A +winged hydrophilic lowland species has many "good" preadaptations for colonization, such as occupation of an unstable habitat including many coastal sites with the potential for high population densities in hydric environments and, of course, the ability to fly.

With 3 montane spp. of *Scarites* on Puerto Rico, additional collecting on Haiti should turn up new species if the area species curve is remotely applicable to montane scaritine faunas (but see comments on ecological shift). When more data becomes available, I propose that the following model be tested. Major colonizing *Scarites* is a +winged form which burrows in a variety of shore and lowland habitats. It disperses to similar habitats on neighboring islands and subsequently invades the montane zone where −wings and flight mechanism atrophy occur along with ecological shift. Evidence for this interpretation could be obtained from detailed analysis of widely distributed +winged lowland forms. *Colpodes estriatus* Darlington and its allies probably represent a distinct genus (Darlington 1939, p. 95). Then, of the three taxa represented in the mountains of Puerto Rico and Hispaniola by a −winged species one, *Oxydrepanus*, is widely distributed in the lowlands of the Greater Antilles; *O. rufus* (Putz.) is known from Cuba, Jamaica and Florida, and *O. micans* Putz. from Hispaniola and Puerto Rico; both species

+ winged. A second montane species, *O. reichoides* Darl., occurs on Hispaniola.

The sophisticated taxonomy necessary to separate monophyletic from polyphyletic origins of —wings in closely related lower categories does not now exist for *Scarites*. Until a more refined systematics becomes available, I think it heuristic and economical to view the biogeography of *Antilliscaris* in light of the model presented above.

PRELIMINARY EVOLUTIONARY DIAGNOSIS: From an assumed lowland, winged and burrowing ancestor, *Antilliscaris* has entered the montane rain forests of Puerto Rico, become flightless, undergone an ecological shift from burrowing to ground crawling, and speciated.

REFERENCES CITED

BANNINGER, M.
    1935. Uber alte und neue formen der Scaritina. *Ent. Blatt.* 1935: 148-160.
    1937-39. Monographie der subtribus Scaritina (Col. Carab.). Pt. I — *Deutsche Ent. Zeitschr.* 1937: 6-160. Pt. II — *Deutsche Ent. Zeitschr.* 1938: 41-181. Pt. III — *Deutsche Ent. Zeitschr.* 1939: 126-161.
    1949. Uber Carabinae. Mittellungen der Münchner. *Ent. Gesellschaft.*
DARLINGTON, P. J., JR.
    1939. West Indian Carabidae V. New forms from the Dominican Republic and Puerto Rico. *Mem. Soc. Cubana Hist. Nat.* 13: 79-101.
    1941. West Indian Carabidae VI. The Jamaican species and their wings. *Psyche* 48: 10-15.
    1943. Carabidae of mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings. *Ecol. Monog.* 13: 37-61.
HLAVAC, T. F.
    1967. Observations on behavior in *Scarites*. *Col. Bull.* 21: 18-22.
LARSEN, O.
    1966. On the morphology of a function of the locomotor organs of the Gyrinidae and other Coleoptera. *Opus. Ent. Supp.* 30: 1-241.
MACARTHUR, R. H., and E. O. WILSON
    1967. The theory of island biogeography. Princeton U. Press, 203 pp.
MUTCHLER, A. M.
    1934. New species of Carabidae from Puerto Rico. *Amer. Mus. Nov.* No. 686, 5 pp.
SMITH, D. M.
    1964. The structure and development of flightless Coleoptera: a light and electron microscopic study of wings, thoracic exoskeleton and rudimentary flight musculature. *J. Morph.* 114: 107-184.